

A NEW SPECIES OF ANEMONE (RANUNCULACEAE) FROM CENTRAL TEXAS

CARL S. KEENER

*208 Mueller Laboratory
Pennsylvania State University
University Park, PA 16802, U.S.A.*

BRYAN E. DUTTON

*Department of Botany
University of Maryland
College Park, MD 20742, U.S.A.*

ABSTRACT

Five species of *Anemone* with tuberous rootstocks occur in Texas: *Anemone caroliniana* Walter, *A. berlandieri* Pritzell, *A. tuberosa* Rydberg, *A. edwardsiana* Tharp, and a new species, *A. okennonii* Keener & Dutton, endemic mainly to the Edwards Plateau in west-central Texas.

RESUMEN

Existen en Texas cinco especies de *Anemone* con rizomas tuberosos: *Anemone berlandieri* Pritzell, *A. caroliniana* Walter, *A. edwardsiana* Tharp, *A. tuberosa* Rydberg, y una nueva especie *A. okennonii* Keener & Dutton endémica principalmente de la Meseta Edwards en el centro-oeste de Texas

INTRODUCTION

The genus *Anemone* L. consists of ca. 150 species of perennial herbs featuring one or more radical leaves, involucrate peduncles, petaloid sepals, and achene fruits. In a recent preliminary reclassification based on restriction site variation and morphology of the subgeneric taxa of *Anemone*, Hoot et al. (1994) recognized two subgenera and seven sections. Section *Anemone* consists of four taxonomically unnamed groups, one of which (the *Coronaria* group) is characterized by distinctive tuberous rootstocks, typically heteromorphic 1–3 ternate radical leaves, simple or branched scapes with sessile involucre bracts positioned near the middle of the peduncle, numerous linear to obovate sepals, and numerous, usually densely woolly achenes borne in ellipsoidal to cylindroidal heads. According to Hoot et al. (1994), the ca. 18 species of the *Coronaria* group of section *Anemone* range from southern Europe to Mongolia, central and southern United States and adjacent Mexico, and South America below 10° south latitude (Hoot 1991; Joseph and Heimburger 1966).

Texas has five species of anemones with tuberous rootstocks: *A. caroliniana* Walter, *A. berlandieri* Pritzel, *A. tuberosa* Rydberg, *A. edwardsiana* Tharp, and a new species, *A. okennonii* Keener & Dutton, herein described from the Edwards Plateau. The aim of our paper is to clarify the taxonomy of these species of *Anemone* in Texas, to provide keys to the taxa, and to describe the new species. Joseph and Heimbürger (1966) reviewed the cytotaxonomic structure of these species (except *A. okennonii*), and provided (p. 908) a helpful comparative chart and distribution maps; the reader is referred to their paper for additional details. The five species treated herein are distinguished chiefly on the basis of leaf dissection, scape pubescence, relative similarity of involucral bracts to the basal leaves, style length, and sepal number and size (see Table 1 for additional details).

Until the species of *Anemone* with tuberous rootstocks are studied world-wide, it would be premature to speculate on phylogenetic relationships of the species treated in our paper (See Hoot et al. [1994] for further analysis of this problem). We believe, however, that *Anemone okennonii* is taxonomically closest to *A. edwardsiana*, but whether these two species are closest phylogenetically remains in question.

KEY TO TEXAS SPECIES OF ANEMONE WITH TUBEROUS ROOTSTOCKS

- 1. Involucre below middle of scape at anthesis; scape nearly glabrous below involucre; involucral bracts similar to at least some radical leaves; styles as long or longer than the ovoid achenes 1. *A. caroliniana*
- 1. Involucre above middle of scape at anthesis; scape glabrous to pubescent below involucre; involucral bracts dissimilar or similar to radical leaves; styles less than half as long as the orbicular, flat achenes.
 - 2. Scape simple, bearing 1 flower; involucral bracts distinctly dissimilar to radical leaves; scape densely pubescent below involucre 2. *A. berlandieri*
 - 2. Scape usually branched, bearing 2 or more flowers per stem; involucral bracts similar or dissimilar to radical leaves; scape nearly glabrous to glabrous below involucre.
 - 3. Involucral bracts similar to radical leaves; radical leaflets narrow, 1–2 cm wide; achenes 3–4 mm wide; rare in Texas (El Paso Co.) 3. *A. tuberosa*
 - 3. Involucral bracts dissimilar to radical leaves; radical leaflets broader, 1.5–2.5 cm wide; achenes 2–3(3.5) mm wide; uncommon, central to western Texas.
 - 4. Leaves 1(2) ternate; leaflets usually crenate-dentate; lateral flowering branches maturing usually at the same time as the central; sepals 10–20, oblanceolate, 2–3 mm wide 4. *A. edwardsiana*
 - 4. Leaves (2)3 ternate; leaflets usually incised with sharp teeth; lateral flowering branches maturing much later than the central; sepals 7–11, oblong, 3–4.5 mm wide 5. *A. okennonii*

1. *Anemone caroliniana* Walter, Fl. Carol. 157–158. 1788.

Slender, apically villous herbs; stems simple, 0.5–3.5 dm tall at anthesis, from rhizomes bearing a series of small, ±oblong to globose tuberous rootstocks 0.5–1 cm long and 0.5 cm thick. Radical leaves 1–2 ternate, to 3.5 cm wide; petioles 3–9 cm long. Leaflets 1–2 cm wide, glabrous, deeply 2–3-parted or divided, segments variously cleft, lobed or toothed, ultimate segments broad to narrow with crenate-dentate margins to variously linear with acute tips, sessile to long petiolulate. Involucral bracts usually similar to at least some radical leaves, reduced, opposite or whorled, sessile to subsessile, sparsely pilose, positioned below middle of scape at anthesis. Flowers solitary; scape villous above involucre, nearly glabrous below. Sepals 10–30, greenish white or pink to purplish blue, linear-oblong, 10–20 mm long and 1–6.5 mm wide; anthers yellow, 0.5–0.75 mm long. Fruiting heads ellipsoidal, to 2 cm long and 1.5 cm broad; achenes brownish, turgid, ±ovoid, ca. 2 mm wide, densely woolly; styles greenish (lavender-tipped), erect, filiform, as long as or longer than achenes, projecting beyond the woolly tomentum; $2n=16$ (Joseph and Heimbürger 1966).

February to April. Prairies, moist sandy soils, calcareous dry grasslands, rocky hillsides, and alluvial flats, South Dakota to Texas, east to South Carolina and Georgia.

Anemone caroliniana is distinguished by its rhizomatous rootstocks bearing a series of small tubers, its heteromorphic radical leaves some of which resemble the involucral bracts, its simple scape bearing involucral bracts below the middle, its scape pubescent above the involucre but glabrous below, and its densely woolly ovoid achenes bearing relatively long styles (Table 1). In Texas, *A. caroliniana* occurs chiefly in the eastern third of the state, with some populations in the west-central and northern regions (see Joseph and Heimbürger 1966, Fig. 3, for a distribution map of this species).

2. *Anemone berlandieri* Pritzl, Linnaea 15:628–629. 1841.

A. heterophylla Nuttall, nomen nudum in syn., Torrey & A. Gray, Fl. N. Amer. 1:12. 1838.

A. caroliniana Walter var. *heterophylla* Torrey & A. Gray, Fl. N. Amer. 1:12. 1838.

A. decapetala Arduino var. *heterophylla* (Torrey & A. Gray) Britton & Rusby, Trans. New York Acad. Sci. 7:7. 1887.

Similar to, though often larger than *A. caroliniana*. Stems simple, (1)3–5 dm tall at anthesis, from thick clavate to oblong, tuberous rootstocks 2–4 cm long and ca. 1 cm thick. Radical leaves 1(2) ternate; petioles 3–20 cm long. Leaflets 2–4 cm wide, pubescent, often 2–3 lobed or parted, the cuneate segments usually broad or rounded apically with dentate or serrate to crenate margins, sessile to long petiolulate. Involucral bracts dissimilar to radical leaves, ultimately dissected into linear segments with acute tips,

TABLE 1. Comparison of Texas *Anemone* species with tuberous rootstocks.

<i>Anemone</i>	<i>caroliniana</i>	<i>berlandieri</i>	<i>tuberosa</i>	<i>edwardsiana</i>	<i>okennonii</i>
STEM					
height (dm)	0.5–3.5	(1)3–5	1–3	3–5	2–3
branches	none	none	1 (rarely 2)	1–3	1–3
time of flowering			central before lateral	lateral with central	central before lateral
PUBESCENCE					
above involucre	villous	villous	villous	densely villous	villous
below involucre	±glabrous	villous	subglabrous	subglabrous	glabrous to subglabrous
TUBEROUS ROOTSTOCKS					
shape	±oblong to globose	clavate to oblong	oblong-obovate	oblong-obovate	oblong-obovate
length (cm)	0.5–1.0	2–4	1.5–2.0	2–4	1–3
thickness (cm)	0.5	1	1	1–2	1
RADICAL LVS					
divisions	1–2 ternate	1(2) ternate	1–2 ternate	1(2) ternate	(2)3 ternate
leaflet width (cm)	1–2	2–4	1–2	2–2.5	0.5–1.5(2.5)
pubescence	glabrous	pubescent	subglabrous	glabrous	subglabrous; marginally ciliate
petiole length (cm)	3–9	3–20	5–7	8–15	5–10
BRACTS					
position	below mid-scape	above mid-scape	above mid-scape	above mid-scape	above mid-scape
pubescence	sparsely pilose	pubescent	thinly pilose	glabrous to sparsely pilose	appressed pilose
sessile/petiolate similar to basal leaves	±sessile yes (some)	sessile no	short-petiolate yes	sessile no	short-petiolate no
SEPALs					
number	10–30	7–17	8–10	10–20	7–11
shape	linear-oblong	linear-oblong	linear-oblong	oblanceolate	oblong
length (mm)	10–20	7–15(20)	10–14	10–16	6–12
color	various	various	greenish white to purplish	greenish white to bluish	greenish white
FRUITING HEAD					
shape	ellipsoidal	cylindroidal	±cylindroidal to ellipsoidal	ellipsoidal cylindroidal	oblong-ellipsoidal
length/width (cm)	1.5–2/0.5–1.5	2–3.5/0.5–1.3	1.5–3/1–1.5	1.5–3/0.6–0.8	1–3/0.5–1
ACHENES					
shape	turgid, ± ovoid	flat, orbicular	flat, orbicular	flat, orbicular	flat, ovate
width (mm)	ca. 2	2–3	3–4	2–3(3.5)	2–3
pubescence	densely woolly	densely woolly	densely villous	sparse	densely white

TABLE 1. continued

<i>Anemone</i>	<i>caroliniana</i>	<i>berlandieri</i>	<i>tuberosa</i>	<i>edwardsiana</i>	<i>okennonii</i>
STYLES					
shape	filiform	subulate	filiform	filiform	filiform
style/ach. length	≥1.0	ca. 1/3	<1/2	ca. 1/3	ca. 1/4
ANTHESIS	Feb. to Apr.	Feb. to Apr.	Apr. to May	Feb. to Apr.	Mar. to Apr.
HABITAT	moist acid soils and calcareous prairies	moist alkaline soils	high dry rocky slopes	canyons, in moist shaded alkaline soils	high dry open ledges and slopes

pilose, positioned above middle of scape at anthesis. Flowers solitary; scape villous throughout. Sepals 7–17, greenish white to pink or purplish blue, linear-oblong, to 7–15(20) mm long and 1.5–5 mm wide; anthers yellowish brown, 0.5–1 mm long. Fruiting heads cylindroidal, 2–3.5 cm long and 0.5–1.3 cm broad; achenes flat, orbicular, 2–3 mm wide, densely woolly; styles greenish (lavender-tipped), subulate with bent tips, ca. 1/3 length of achenes, not projecting beyond the dense woolly tomentum; 2*n* = 16 (Joseph and Heimburger 1966).

February to April. Limestone hills, grassy knolls, and stony ground, Texas and Oklahoma eastward to (rarely) North and South Carolina.

Anemone berlandieri is distinguished by its ternate radical leaves with broad segments having typically crenately toothed margins, its simple scape bearing involucral bracts above the middle of the more or less uniformly pubescent scape, its bracts distinctly unlike the radical leaves, and its densely woolly orbicular, flat achenes bearing styles ca. 1/3 length of the achene (Table 1). In Texas, *A. berlandieri* occurs throughout the state except for the extreme western portions (i.e., High Plains and Trans-Pecos, Mountain and Basin regions; see Map 1, Correll and Johnston 1970).

The taxonomy of this species is complicated, owing largely to whether the North American plants are conspecific with the South American species recognized as *A. decapetala* Arduino (Britton 1891), and the adoption of the name *A. heterophylla*, which is listed by Torrey and A. Gray (Fl. N. Amer. 1:12. 1838) merely as a synonym for *A. caroliniana* Walter var. *heterophylla* Torrey & A. Gray. Joseph and Heimburger (1966) clarified distinctions between the North and South American species, and Keener (1975) reviewed the legitimacy of the name *A. heterophylla*.

3. *Anemone tuberosa* Rydberg, Bull. Torrey Bot. Club 29:151–152. 1902.

A. sphenophylla sensu Britton, Ann. New York Acad. Sci. 6:220. 1891, p.p., non Pöppig, Frag. syn. 27. 1833.

Robust, apically villous herbs; stems simple below, usually branched above involucre, 1–3 dm tall at anthesis, from brownish, oblong-obovate tuberous rootstocks 1.5–2 cm long and 1 cm thick. Radical leaves several, 1–2 ternate; petioles 5–7 cm long. Leaflets 1–2 cm wide, subglabrous, variously parted or cleft, with cuneate-obovate segments having acute tips, sessile to petiolulate. Involucral bracts 3, similar to radical leaves in dissection, reduced, short-petiolate, thinly pilose, positioned above middle of scape at anthesis; secondary branches 1 or more, 2-bracteate. Flowers 1-several per scape; lateral flowering branches maturing later than central flower; scape villous above involucre, subglabrous below. Sepals 8–10, greenish white to purplish, linear-oblong, 10–14 mm long, 3–6.5 mm wide; anthers yellowish brown, ca. 1 mm long. Fruiting heads cylindroidal to ellipsoidal, 1.5–3 cm long and 1–1.5 cm broad; achenes flat, orbicular, 3–4 mm wide, densely villous; styles lavender, \pm erect, filiform, less than 1/2 length of achenes, not projecting beyond the dense woolly tomentum; $2n=16$ (Joseph and Heimbürger 1966).

April to May. High dry rocky slopes, southeastern California, southern Nevada, and southwestern Utah, southeastward to extreme western Texas (El Paso Co.), where it occurs on igneous rocky slopes (Joseph and Heimbürger 1966).

Anemone tuberosa is distinguished by its ternate to biternate radical leaves with acute-tipped oblong-ovate segments, its relatively large involucral bracts similar in dissection to the radical leaves, its typically branched scape with an involucre above the middle at anthesis, its scape pubescent above the involucre but more or less glabrous below, and its densely villous, flat, orbicular, achenes having styles less than 1/2 the length of the achene (Table 1).

Britton (1891) regarded the North American populations conspecific (as *A. sphenophylla*) with similar populations in Chile, but Rydberg (1902) pointed out that in the Chilean plants “the whole scape is decidedly pubescent with ascending hairs and the segments of the involucral bases are narrower.” However, Lourteig (1951: 564) regarded *A. sphenophylla* as a taxonomic synonym of *A. decapetala* Arduino.

4. *Anemone edwardsiana* Tharp, Amer. Midl. Naturalist 33:669. 1945.

Slender, apically villous herbs; stems simple below, usually branched above involucre, 3–5 dm tall at anthesis, from brownish, oblong-obovate tuberous rootstocks 2–4 cm long and 1–2 cm thick. Radical leaves several to many, 1(2) ternate; petioles 8–15 cm long. Leaflets reniform in outline, 2–2.5 cm wide, glabrous, variously 2–4 cleft, lobes crenate-dentate to sharply toothed, sessile to petiolulate. Involucral bracts 3, \pm sessile, dissimilar to radical leaves, 2–5 cm long, ultimately dissected into oblanceolate

segments with rounded to acute tips, glabrous to sparsely pilose, positioned above middle of scape at anthesis; secondary branches 1–3, 2-bracteate. Flowers 1-several per scape; lateral flowering branches usually maturing with central flower; scapes villous above involucre, subglabrous below. Sepals 10–20, greenish white to bluish, oblanceolate, 10–16 mm long, 1.5–3(4) mm wide; anthers bright yellow, 0.5–1 mm long. Fruiting heads ellipsoidal to cylindroidal, 1.5–3 cm long and 0.6–0.8 cm broad; achenes flat, orbicular, 2–3(3.5) mm wide, typically sparsely pubescent to glabrous; styles erect to horizontal, filiform, ca. 1/3 length of achenes, not projecting beyond the woolly tomentum; $2n=16$ (Joseph and Heimburger 1966).

February to April. Alkaline soils in moist shaded canyons; shaded, moist, rocky limestone bluffs and ledges along eastern edge of Edwards Plateau (R.J. O’Kennon, pers. comm.). Two varieties:

- a. Achenes woolly, ±dull var. *edwardsiana*
- a. Achenes glabrous, vernicose (polished) var. *petraea*

4a. *Anemone edwardsiana* var. *edwardsiana*

Range and habitat of the species.

4b. *Anemone edwardsiana* var. *petraea* Correll, Madroño 19:189. 1968.

Tall, spindly plants with glabrous, vernicose achenes endemic to moist rocky crevices along Curry Creek near Kendalia, Kendall Co., Texas. Additional population and cytotaxonomic studies are desirable to establish more clearly the range of this taxon as well as its phylogenetic relationships to other species in this complex.

The most polymorphic of Texas anemones, *A. edwardsiana* combines features of both *A. tuberosa* and *A. berlandieri* (cf. Table 1). It is like *A. tuberosa* in having a branched scape glabrous or slightly pubescent below the involucre, and like *A. berlandieri* in having involucre bracts with long, narrow, sharply toothed segments quite dissimilar from the radical leaves. Achene shape, style length, and position of the involucre bracts are similar to those character states in both *A. berlandieri* and *A. tuberosa*. The combination of branched scapes, involucre bracts dissimilar to the radical leaves, and relatively few sparsely woolly to glabrous achenes demarks *A. edwardsiana* from the other anemones in Texas.

Joseph and Heimburger (1966) pointed out that *A. edwardsiana* not only combines features of *A. tuberosa* and *A. berlandieri* (= *A. heterophylla* in their treatment), but also “shows an intermediate geographic range and altitude preference.” They suggested that *A. edwardsiana* may be a hybrid derivative of *A. tuberosa* and *A. berlandieri*. However, based on restriction site analyses, Hoot et al. (1994) claimed that *A. edwardsiana* is a sister species to *A.*

berlandieri and possesses "no rDNA fragments in common with *A. tuberosa*." Additional biosystematic studies are desirable to clarify the phylogenetic relationships of this complex.

Because of glabrous, vernicose achenes, Correll (1968) segregated several populations occurring near Kendalia in Kendall Co., Texas, as *A. edwardsiana* var. *petraea* Correll. These populations appear to be an ecotypic phase of the polymorphic *A. edwardsiana*.

5. *Anemone okennonii* Keener & Dutton, sp. nov. (Figs. 1,2)

Herba perennis erecta e tuberibus brunneis; tubera oblongo-obovata, 1–3 cm longa, 1 cm crassa. Folia radicalia pluria, triternata, glabriuscula; petioli usque ad 10 cm longi. Foliola 0.5–1.5 (2.5) cm lata, profunde 2–4-fida; lobi cuneati-acuti; petioluli usque ad 2 cm longi. Scapi 2–3 dm alti, basibus glabratis, apicibus pubescentibus; bracteae primariae involucri 3, 2–5 cm longae; ramuli axillares (0)1–2(3), unusquisque involucri secundario bi-bracteato. Flores centrales 1.5–2.5 cm lati; ceteri parviores; sepala viridi-alba. Capitula fructificantia oblongo-elliptica, 1–3 cm longa. Achenia lata, ovata, marginata, brevirostria; rostra plus minusve erecta, pilis basibus sub-aequantibus corpora pubescentia.

Slender, apically villous herbs; stems simple below, usually 1–3 branched above involucre, 2–3 dm tall at anthesis, from brownish oblong-obovate tuberous rootstocks 1–3 cm long and 1 cm thick. *Radical leaves* several to many, (2)3 *ternate*; petioles 5–10 cm long. *Leaflets* 0.5–1.5(2.5) cm wide, subglabrous but marginally ciliate, deeply 2–4 cleft, *lobes cuneate-acute, reddish-glandular*; petiolules to 2 cm long. Primary involucre bracts 3, short-petiolate, dissimilar to radical leaves, 2–5 cm long, variously cleft into linear, acute-tipped segments, appressed pilose, positioned above middle of scape at anthesis; secondary branches (0)1–2(3), 2-bracteate. Flowers 2–several per scape; *lateral flowering branches maturing later than central flower*; scapes pubescent above involucre, glabrous or subglabrous below. *Sepals* 7–11, *greenish white, oblong, 6–12 mm long, (2)3–4.5 mm wide; anthers pale yellow, fading to creamy brown, 0.75–1 mm long*. Fruiting heads oblong-ellipsoidal, 1–3 cm long and 0.5–1 cm broad; *achenes* flat, ovate, 2–3 mm broad, *densely white villous; styles lavender-tinted, ±erect to horizontal, filiform, ca. 1/4 length of achenes*, not projecting beyond the wooly tomentum. Chromosome number unknown.

TYPE: U.S.A. TEXAS. Gillespie Co.: high on shallow roadcut in sandy loam, Fm 783, 2 mi S of Doss, 22 Apr 1993, *Robert J. O'Kennon* 11390 (HOLOTYPE: BRIT; ISOTYPES, PAC, TEX; see Fig. 1). Named in honor of its discoverer, Robert J. O'Kennon, keen student of the flora of Texas.

Representative specimens examined: U.S.A.: TEXAS: **Brewster Co.**: Glass Mts., 21 Mar 1941, *Rose-Innes & Warnock* 565 (SMU). **Crockett Co.**: 14.8 mi W of Ozona, 14 Mar 1949, *Turner & Warnock* 273 (SMU). **Kimble Co.**: Hwy 385, 2.5 mi S of Llano River, 9 Mar 1992, *R. J. O'Kennon* 8813 (PAC). **Mitchell Co.**: Lake Hollywood, 27 Mar 1945, *Pohl* 4744 (SMU). **Pecos Co.**: 20 mi NE of Ft. Stockton toward McCamey, 27 Apr 1947, *Warnock* 5199 (SMU).

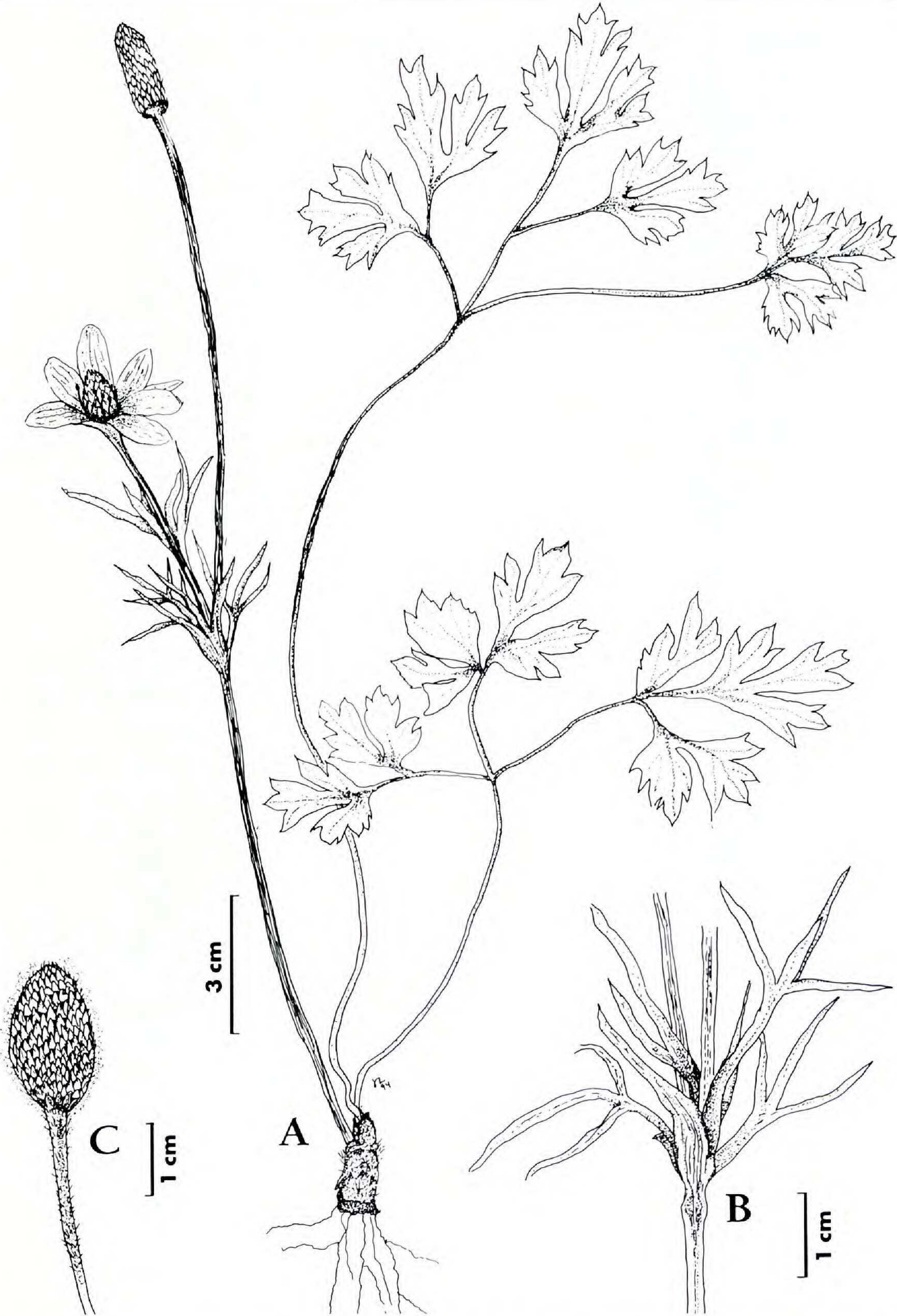


FIG 1. *Anemone okennonii* from the holotype. A) habit; B) primary involucre bracts; C) fruiting head.



FIG. 2. Habit of *Anemone okennonii*.

Terrell Co.: 31 mi S of Sheffield, 14 Mar 1949, *Turner & Warnock* 307 (SMU); 4.2 mi W of Sanderson, 14 Mar 1949, *Turner & Warnock* 319 (SMU). **Val Verde Co.:** 20 mi NNW of Del Rio, 31 Mar 1947, *McVaugh* 7729 (SMU).

March to April. Dry sunny rocky limestone ledges, hills, and roadsides, in red sandy loam and igneous-based soils at an elevation of 490–530 m. Endemic from Gillespie and Mitchell cos., southwestward to Val Verde and Brewster cos., Texas, mainly in the Edwards Plateau vegetational area with outliers in the Rolling Plains and Trans Pecos, Mountain and Basin vegetational areas (see Map 1, Correll and Johnston 1970).

Anemone okennonii has been variously recognized as *A. caroliniana* Walter, *A. decapetala* Arduino, *A. edwardsiana* Tharp, *A. sphenophylla* Pöppig, *A. tuberosa* Rydberg, or possibly a hybrid between *A. tuberosa* and *A. heterophylla* Nuttall (= *A. berlandieri* Pritzel).

Anemone okennonii differs from its nearest presumed congener, *A. edwardsiana*, by its leaf dissection ([2]3 ternate vs. 1[2] ternate), its smaller leaflets (0.5–1.5 cm wide vs. 2–2.5 cm wide) with sharply cleft (rounded) lobes, its central flower maturing before (with) the lateral flowers, its sepal number (7–11 vs. 10–20), anther color (pale yellow vs. bright yellow), achene pubescence (densely white villous vs. sparse to glabrous), seedling leaves (similar to basal leaves vs. similar to bracts), relatively later blooming period (March to April vs. February to April), and habitat (drier, more exposed sites vs. more moist and shaded sites). The following chart summarizes differences between *A. okennonii* and other Texas species of *Anemone* with tuberous rootstocks:

1. Radical leaves typically 3-ternate	Distinctive
2. Leaves reddish-glandular on margins, tips	Distinctive
3. Leaf divisions cuneate-acute	Like <i>A. tuberosa</i>
4. Smaller flowers (cf. sepal length, below)	Distinctive
5. Two or more flowers per stem	Like <i>A. edwardsiana</i> and <i>A. tuberosa</i>
6. Central flower matures before lateral flowers	Like <i>A. tuberosa</i>
7. Anthers pale yellow, fading to creamy brown	Distinctive
8. Styles lavender-tinted	Distinctive
9. Involucre with linear divisions	Like <i>A. berlandieri</i>
10. Sepals 7–11	Like <i>A. tuberosa</i>
11. Sepals oblong, 6–12 mm × (2)3–4.5 mm	Distinctive

Plant associates of *A. okennonii* include *Acacia roemeriana* Scheele, *Aristolochia coryi* I.M. Johnston, *Colubrina texensis* (Torrey & A. Gray) A. Gray, *Delphinium carolinianum* Walter, *Draba cuneifolia* Torrey & A. Gray, *Echinocereus enneacanthus* Engelm., *Euphorbia acuta* Engelm., *Ferocactus setispinus* (Engelm.) L. Benson, *Gilia rigidula* Benth., *Haplopappus spinulosus* (Pursh) DC., *Melampodium leucanthum* Torrey & A. Gray, *Opuntia phaeacantha* Engelm., *Prunus minutiflora* Engelm., *Tetraclea coulteri* A. Gray, and *Thamnosma texana* (A. Gray) Torrey (R. J. O'Kennon, pers. comm.).

Anemone okennonii appears to have evolved from *A. edwardsiana* and may

actually be a xeric form of it (R. J. O'Kennon, pers. comm.). O'Kennon has suggested (pers. comm.) that millions of years ago when western Texas was more mesic than at present a precursor form of *A. edwardsiana* was most likely the predominant species of *Anemone* in this area. As western Texas became hotter and drier (and this trend continues at present), xeric forms began to evolve. *Anemone tuberosa* probably evolved first farther west, and then *A. okennonii* evolved to fit into the niche between the two. The three species seem not to overlap anywhere in their ranges. The only species sympatric with *A. okennonii* is *A. berlandieri*, but there does not appear to be any intergradation between these two species. Critical biosystematic and population studies would be useful in establishing the most probable phylogenetic relationships among these five taxa of Texas anemones with tuberous rootstocks.

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REFERENCES

- BRITTON, N.L. 1891. The American species of the genus *Anemone* and the genera which have been referred to it. Ann. New York Acad. Sci. 6:215–238.
- CORRELL, D.S. 1968. Some additions to the flora of Texas—IV. Madroño 19:187–192. [Type description of *Anemone edwardsiana* Tharp var. *petraea* Correll, 189.]
- _____ and M.C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner.
- HOOT, S.B. 1991. Phylogenetic relationships in *Anemone* based on morphology and chloroplast DNA variation. Ph.D. dissertation, Univ. of Michigan.
- _____, A.A. REZNICEK and J. PALMER. 1994. Phylogenetic relationships in *Anemone* (Ranunculaceae) based on morphology and chloroplast DNA. Syst. Bot. 19:169–200.
- JOSEPH, C. and M. HEIMBURGER. 1966. Cytotaxonomic studies on New World species of *Anemone* (Section *Erioccephalus*) with tuberous rootstocks. Canad. J. Bot. 44:899–928.
- KEENER, C.S. 1975. Studies in the Ranunculaceae of the southeastern United States. I. *Anemone* L. Castanea 40:36–44.
- LOURTEIG, A. 1951. Ranunculáceas de Sudamérica templada. Darwiniana 9:397–608.
- RYDBERG, P.A. 1902. Studies on the Rocky Mountain flora—VII. Bull. Torrey Bot. Club 29:145–160. [Type description of *Anemone tuberosa* Rydberg, 151–152.]